Distribution of *Volvarina hennequini* Boyer, 2001 in the Western Caribbean Sea and description of a new bathyal *Volvarina* from Northern Colombia

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ABSTRACT. New records of *Volvarina hennequini* Boyer, 2001 from bathyal levels off Eastern Panama and Northern Colombia are documented and the distribution pattern of this species in the Western Caribbean Sea is discussed. *V. bayeri* sp. nov., obtained from a similar bathyal level off the Peninsula de la Guajira, is described and the question of the diversity of the Marginellidae at bathyal levels in Caribbean Sea is tackled.

INTRODUCTION

In a recent paper, Boyer (2001a) described two new species from the northern slopes of Honduras : *Volvarina bessei* from mid-levels of circalittoral (120-130 m) and *V. hennequini* from upper bathyal depths (420-480 m).
V. hennequini was compared with *V. yucatenaca* (Dall, 1881), a much smaller species found at upper bathyal depths in the Yucatan Strait.
The radula of *V. hennequini* was presented, showing the typical comblike pattern of the genus (32 plates bearing 30 to 36 cusps). The soft parts of a live animal were also pictured, showing the subhyalinous whitish-grey ground commonly found in many species restricted to bathyal or abyssal depths.
The main interest of this species is of biogeographic order, as the bathyal marginellids are practically unrecorded within the Caribbean Sea basin, whereas several species have been discovered since the end of the XIX° century in the Northern Caribbean area (mainly by Dall, from the Gulf of Mexico and Florida) and in Northeast Atlantic (Bouchet & Warèn, 1985).
New records of *V. hennequini* recently obtained from bathyal levels off Northern Colombia and Eastern Panama allow to widely extend the distribution range of the species, but also to precise the issue of the marginellids diversity at deep levels from the Caribbean Sea.
In the course of this study, another species of *Volvarina* ranging at a similar depth off the Peninsula de la Guajira was discovered. It is described herein as new to science.

SYSTEMATICS

Family **Marginellidae** Fleming, 1828
Genus ***Volvarina*** Hinds, 1844
Type species : *Marginella nitida* Hinds, 1844 (subsequent designation by Redfield, 1871), junior synonym of *Volvarina mitrella* (Risso, 1826).

Volvarina hennequini Boyer, 2001
Figs 1-10

Volvarina hennequini Boyer, 2001a : 4-5, 8.

Type material. Holotype in MNHN (14.7 x 6.75 mm), 7 paratypes (adult shells sizing 13.5 x 6.4 mm to 16.1 x 7.8 mm) in A. Wakefield collection, T. Mc Cleery collection and the collection of the author.

Other material examined. Already examined in Boyer (2001a), all coming from the type locality :
- 1 adult shell in P. Lepetit collection,
- 2 adult shells in B. Besse collection,
- 5 juvenile shells in the collection of the author.

New material examined :
- 22 live and dead specimens (18 adults and 4 juveniles) in the INVEMAR collections (Table 1 & Figs 1-10), trawled during the INVEMAR 1998-1999 campaign from 15 stations along the northern coasts of Colombia, from Puerto Escondido to the Peninsula de la Guajira, at depths ranging from 442 to 510 m.
- 3 dead specimens purchased by Tony Mc Cleery to Marcos Alvarez (Panama City), together with a vast amount of microshells supposed to come from several localities situated off the Caribbean and the Pacific coasts of Panama. These 3 adult shells have

unprecise labels : Ref. 200419P031, Montuosas (15.0 x 7.3 mm); Ref. 200411VV001, Southern Caribbean western, deep dredged (15.3 x 7.6 mm); Ref. 200411VVV001, San Blas, deep dredged (16.1 x 8.0 mm). The first of these localities corresponds to Montuosas Islands, situated in the Gulf of Chiriqui, along the western tip of the Pacific coasts of Panama. The second locality could signify "Caribbean coasts of Panama" as well as "Northern Colombia" or "eastern coasts of Costa Rica". The third locality corresponds to the eastern part of the Caribbean coast of Panama (San Blas Gulf and Archipelago).T. Mc Cleery points out (pers. comm.) that the localities attached to the "Alvarez lots" are not reliable, as many of them proved to be incoherent or contradictory.

Type locality. Off Omoa, Northern Honduras. Trawled at 420-480 m.

Description. Shell, animal and radula : in Boyer, 2001a : 5.
Comparing the morphology of the shells at hand, one can observe an evident geographic cline of forms within the species, from squat inflated shells with tall spire in the Bay of Honduras (Boyer, 2001a : figs 9-14) to slender shells with shorter spire off Northern Colombia (Figs. 1-10). The 3 shells said to come from Panama present an intergrading stage, with squat inflated shells and low or moderate spire. The Colombian populations themselves show a tendency to more slender shells towards the northeastern tip of their distribution.

Habitat. In muddy / silty sediments, on bathyal plains.

Distribution. The geographic distribution of *V. hennequini* is proposed here as ranging from the Gulf of Honduras to the Peninsula de la Guajira, and it is supposed to be continuous all along this range at upper bathyal levels. This pattern corresponds to most of the Western Caribbean Sea. An extension of this distribution to the Greater Antilles and to Venezuela based upon new records is not excluded.
The presence of *V. hennequini* off the Pacific coast of Panama is possible, as this area was connected with the Western Caribbean Sea basin until the Pliocene / Pleistocene limit (Petuch, 1988). However, it must be noted that if sibling or closely related species are commonly recorded from both sides of the isthmus, the matter plays clearly for infralittoral and circalittoral items, but it is not so clearly attested for bathyal items. The reason possibly lies in the more limited interoceanic communications at bathyal levels in Central America during upper Pliocene and lower Pleistocene. As a matter of fact, the occurrence of *V. hennequini* in Pacific waters cannot be determined on the basis of a single record coming from a "second hand" purchasing.
The bathymetric distribution of *V. hennequini* seems to be very homogeneous. In the Gulf of Honduras, the species was found in 420-480 m but not in 120-130 m. In the more documented INVEMAR samplings, all specimens of *V. hennequini* were found within a narrow depth range (442 to 510 m), which looks very similar to the zonation recorded from Northern Honduras. Apparently the species does not reach upper levels beyond 400 m, but the possible deeper distribution under 510 m certainly requires further inquiries.

Volvarina bayeri sp. nov.
Figs 11-12

Type material. Holotype (12.98 x 5.07 mm) in INVEMAR, MOL2363 (Figs 11-12), St INV. 002 (E92).

Type locality. Off Bahia Honda, Peninsula de la Guajira. Trawled at 493 m.

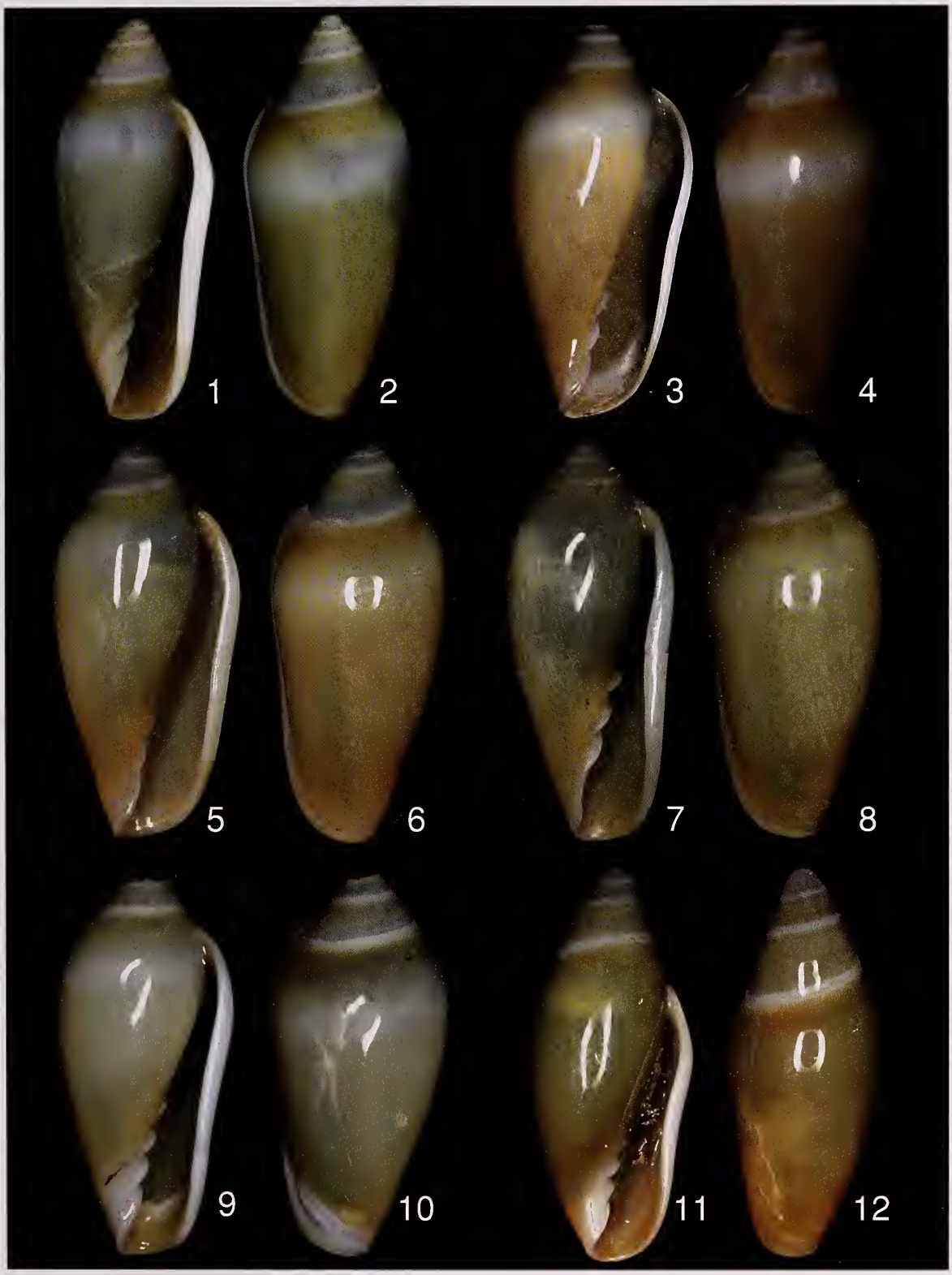
Description. Shell narrow, slender fusiform, spire produced, sizing 35 % of the total length, domed protoconch, 2.5 whorls. Outer lip flexuous, shoulder sloping, aperture narrowed, widening in the anterior part, rounded base, 4 packed oblique columellar plaits.
Colour ground of the body whorl amber, spire more greyish, suture zone, anterior part of the columella and border of the outer lip whitish.
Animal and radula unknown.

Habitat. Muddy bottom.

Distribution. Only known from the type locality.

Figures 1-12

1-10. *Volvarina hennequini.* **1-2.** INV MOL2312, 23.35 x 10.9 mm. **3-4.** INV MOL2315, 20.28 x 9.25 mm. **5-6.** INV MOL1864, 17.70 x 8.13 mm. **7-8.** INV MOL1866, 16.37 x 7.50 mm. **9-10.** INV MOL1869, 16.44 x 8.08 mm.
11-12. *Volvarina bayeri* sp. nov. Holotype INV MOL2363, 12.98 x 5.07 mm.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Remarks. *V. bayeri* sp. nov. and *V. hennequini* both range at similar depths off the Peninsula de la Guajira and they are the single *Volvarina* known from the bathyal levels of the Caribbean Sea basin.

Due to its high uncoiling stretch and to its packed columellar plaits, the shell of *V. bayeri* shows as much distinct from that of *V. hennequini* and both species do not look as close relatives, despite their similar shell decoration (honey amber colour ground, whitish suture zone, outer lip and base of the columella). This situation of similar shell decorations in non-related molluscan species sharing the same environment is quite currently observed in the field, even if it is not well-documented by the literature. It may be interpreted as corresponding to cases of superficial adaptative convergences assuming the same solutions of homochromy.

The bathyal gastropods presenting generally widespread distributions better than restricted ones, one can assume that *V. bayeri* is not endemic from the Peninsula de la Guajira, but may have a wider distribution along the Caribbean Sea basin.

Etymology. From F. M. Bayer, American malacologist who dedicated a special attention to the deep sea mollusks from the Caribbean Sea.

DISCUSSION

Until the description of *V. hennequini*, no bathyal species of Marginellidae was apparently recorded in the literature from the whole Caribbean Sea basin, even when deep levels were especially checked (about Western and Southwestern Caribbean Sea, see Bayer, 1971; Petuch, 1987 & 1988; Diaz & Puyana, 1994).

It must be noted that several species of marginelliform gastropods, including tiny ones, were brought from a circalittoral level (70 m) by INVEMAR samplings during the 1998-2001 campaigns, like *Gibberula pulcherrima* (Gaskoin, 1849), *Gibberula* sp., *Volvarina monicae* Díaz, Espinosa & Ortega, 1996 or *Volvarina avena* (Kiener, 1834), whereas no further marginellid species was yielded from bathyal levels off the Caribbean coasts of Colombia, except *V. hennequini* and *V. bayeri*.

The apparent lack of Marginellidae at bathyal levels in the Caribbean Sea basin may be partially the result of insufficient efforts of sampling at such depths or due to the superficial study of the material preserved in some institutions. One must point out that the bathyal Marginellidae known from Atlantic waters were all collected on the slopes most easily explored by the intensive oceanographic campaigns organized by rich industrial countries (i.e. slopes ranging south and southeast of USA and southwest of Europe), whereas the Atlantic intertropical areas were not sampled in the same conditions. So, it can be supposed that an equivalent effort applied to bathyal levels in Atlantic intertropical areas might bring new species of Marginellidae to science.

However, it is also possible that the diversity of Marginellidae is truly very low at bathyal levels in the Atlantic in general, and in particular under intertropical latitudes. The number of bathyal species of Marginellidae in the Northeast Atlantic (even if most of them are large sized species) seems to be very limited : Bouchet & Warèn (1985: 267-272) listed only 7 bathyal species of Marginellidae in this area. Likewise, a limited number of tiny bathyal species of Marginellidae were recognized from the Floridian and the Carolinian areas by Dall and subsequent authors.

The apparent scarcity of bathyal Marginellidae in the Caribbean Sea basin may be an extension of this phenomenon towards the western tip of the old Tethys Sea. Considering the very important diversity of bathyal marginelliform gastropods (both at generic and specific levels) in New Caledonian waters yielded by the French Expeditions in the last 20 years (Boyer, 2001b & 2002), with an estimate of more than 100 species (mostly Marginellidae *sensu stricto*), one could infer that the bathyal Marginellidae did spread along the Tethys Sea from an originating "mother zone" located in tropical Western Pacific, according to a model of westward declining diversity.

However, the generic composition of the diversity of Marginellidae at bathyal levels is not the same at all in every case. For instance, the bathyal Marginellidae from New Caledonia mostly belong to the genera *Haloginella* (close to the Indo-Pacific "*Serrata* group"), *Protoginella* (close to the Australian "*Mesoginella* group") and *Dentimargo,* whereas the bathyal Marginellidae from the Northeast Atlantic mostly belong to the genus *Marginella.*

Actually, it seems that in both cases the composition of the bathyal diversity is better linked to the composition of the diversity observed at upper levels in the same area. The genus *Dentimargo* is well represented in the infralittoral and the circalittoral of the western and central Indo-Pacific Province, and *Haloginella* as well as *Protoginella* have close relatives in shallower eastern Australasian waters. The same occurs for the bathyal *Marginella* species from the Northeast Atlantic, which have close relatives at upper levels in West African waters. In other words, as far as this family is concerned, the phylogenic relationships of the bathyal Marginellidae seem to depend more on "vertical connections" than on "horizontal connections", and to be established at a regional scale.

The same kind of process seems to occur in the Caribbean Sea basin, as it can be observed that the two only bathyal Marginellidae known from the western side of the basin belong to the most diversified genus of Marginellidae in the Caribbean. If close relatives from upper levels can be proposed for *V. hennequini,* the best candidates (as far as the

shell morphology is concerned) are surely *V. avenella* (Dall, 1881) and overall *V. succinea* (Conrad, 1846), both found in the infralittoral of West Florida. The animal and the radula of *V. succinea* are described by Coovert (1988) : the animal is much decorated compared to the achromatic *V. hennequini,* but the total loss of chromatism is probably of easy contracting for strictly bathyal species. The radula of *V. succinea* is also somewhat different from that of *V. hennequini,* principally because the later shows alternated big and small cusps. However, this feature is not very significant, as some species of *Volvarina* can also show such radular variability at intraspecific level (for instance in the group *V. exilis* Gmelin, currently under study by the second author).

Another question is to know why such a high diversity can be observed in Marginellidae at bathyal levels in the tropical West Pacific and why not in the Caribbean intertropical zone. The answer surely lies in a very intricate complex of causes, probably including the respective influence of the hydroclimatic events, of the size of the considered areas at each historical period, and of the time available for the setting up of the ecologic components and of the phyletic radiations since the last drastic faunal recasting.

Further investigations on the setting up of the bathyal faunas of Marginellidae in the Caribbean Sea, compared to the situation occurring in Indo-Pacific and other Atlantic locations, would be of great interest for a better understanding on the biogeographic history of the Tethyan area.

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NUMBER OF SHELLS	MEASUREMENTS OF THE SHELLS	MUSEUM CATALOG NUMBER	*DATE*	STATION	DEPTH (m)	LAT. N	LONG. W	LOCALITY
2 specimens collected alive (OH 70%) 1 specimen, empty shell	23.35 x 10.9 mm 18.27 x 7.57 mm 21.62 x 9.76 mm adults	INV MOL2312	21-Nov-98	INV.002 (E12) muddy bottoms	442 452	12°31´47.4" 12°31´28"	72°07´45" 72°08´09"	Bahía Honda
1 specimen, empty shell (Dry)	9.54 x 4.48 mm juvenile	INV MOL2313	22-Nov-98	INV.003 (E14) muddy bottoms	446 450	12°29´13.8" 12°29´1.8"	72°15´29.4" 72°15´51"	Bahía Portete
1 specimen collected alive (Dry)	18.70 x 8.30 mm adult	INV MOL2314	24-Nov-98	INV.005 (E19) muddy bottoms	464 468	12°19´5.4" 12°19´13.8"	72°42´52.2" 72°42´28.2"	Cabo de la Vela
1 specimen collected alive (OH 70%)	20.28 x 9.25 mm adult	INV MOL2315	26-Nov-98	INV.010 (E27) muddy bottoms	492 500	11°27´3.6" 11°27´14.4"	73°42´12" 73°41´43.8"	Palomino
1 specimen, empty shell (Dry)	14.71 x 6.55 mm juvenile	INV MOL2316	26-Nov-98	INV.010 (E28) muddy bottoms	496 500	11°27´13.8" 11°27´10.8"	73°42´18.6" 73°41´55.8"	Palomino
5 specimens: 4 empty shells and 1 collected alive* (Dry)	19.36 x 9.05mm 21.57 x 9.15 mm 19.25 x 9.03 mm 21.56 x 9.61 mm 17.95 x broken* adults	INV MOL2317	27-Nov-98	INV.012 (E32) muddy bottoms	488 492	11°27´23.41 11°27´18"	73°51´53.4" 73°52´19.2"	Río Piedras
2 specimens collected alive (OH 70%)	17.45 x 7.47 mm 16.35 x 7.36 mm	INV MOL2386	01-Dec-98	INV.013 (E34)	500 510	11°26´46.2" 11°26´33.6"	74°01´31.2" 74°01´57"	Chengue
1 specimen collected alive (OH70%)	17.70 x 8.13 mm adult	INV MOL1864	07-Dec-98	INV.024 (E52) muddy bottoms	492 490	11°07'56" 11°08'06"	75°13´38" 75°13´12"	Bocas de Ceniza
1 specimen collected alive (OH 70%)	The specimen was broken.	INV MOL1865	07-Dec-98	INV.025 (E53) muddy bottoms	490 482	11°06'55" 11°07'14"	75°08´15" 75°08´33"	Bocas de Ceniza
2 specimens collected alive (OH 70 %)	16.37 x 7.50 mm adult 12.06 x 5.54 mm juvenile	INV MOL1866	07-Dec-98	INV.025 (E54) muddy bottoms	502	11°07'5.4" 11°07'7.8"	75°07´47" 75°07´26"	Bocas de Ceniza
1 specimen, empty shell (Dry)	17.12 x 8.01 mm adult	INV MOL2318	23-Mar-01	INV.068 (E142)	487	10°31´66" 10°31´26"	75°39´05" 75°39´07"	Cartagena
1 specimen, empty shell (Dry)	16.44 x 8.08 mm adult	INV MOL1869	13-Apr-99	INV.031 (E71)	490 484	09°53'19" 09°52'55"	76°13´59" 76°14´ 05"	NW Islas de San Bernardo
1 specimen, empty shell (Dry)	14.40 x 6.52 mm juvenile	INV MOL1868	10-Apr-99	INV.034 (E65)	498 480	09°30'27" 09°29'58"	76°26´46" 76°26´43"	Ensenada de la Rada
1 specimen, empty shell (Dry)	15.58 x 7.30 mm adult	INV MOL1867	09-Apr-99	INV.036 (E61)	490 500	09°18'52" 09°18'26"	76°29´37" 76°29´48"	Puerto Escondido

Table 1. Records of *Volvarina hennequini* from INVEMAR samplings.